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To what extent are bryophytes efficient dispersers?

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Abstract

- Bryophytes are typically seen as extremely efficient dispersers. Experimental evidence suggests that efficient short- and long-distance dispersal coupled with random colonization leads to an inverse isolation effect. Under the latter, a higher genetic diversity of colonizing propagules is expected with increasing isolation, counteracting differentiation beyond the range of short-distance dispersal.
- This expectation is tested from a review of evidence on spatial genetic structure and analyses of isolation-by-distance (IBD) at different scales.
- A decay of the IBD signal, characterized by non-significant slopes between kinship coefficients and distance, was observed in 2/3 of the investigated datasets beyond 100m. A second slope shift was observed at distances larger than 100km, with a proportion of significant slopes in >50% of the datasets.
- The decay of the IBD signal beyond 100m, which reflects the rapid decrease of spore densities with increasing distance from the source, is consistent with the inverse isolation hypothesis. Persistence of a significant IBD signal at medium ranges in 1/3 of the cases suggests, however, that the inverse isolation effect is not a rule in bryophyte spore dispersal. Furthermore, the higher proportion of significant isolation-by-distance patterns observed at scales over 100km likely marks the limits of regional dispersal, beyond which an increasingly smaller proportion of spores travel.
- We discuss the differences between experimental and genetic estimates of spore dispersal and conclude that geographic distance remains a significant proxy of spore colonization rates, with major consequences for our understanding of actual migration capacities in bryophytes, and hence, our capacity to model range shifts in a changing world.

Introduction

Dispersal is a central evolutionary process. Obtaining unbiased estimates of the distribution of dispersal distances in natural unbounded populations has, however, long been a challenging issue (Koenig, Van Vuren, & Hooge, 1996). Dispersal can be assessed in two ways. Direct techniques implement descriptions of dispersal kernels from local measurements derived, for instance, from trapping experiments, and then extrapolate the potential for dispersal broadly beyond the scale of measurements, in both time and space. Indirect techniques are based on inferences from spatial genetic structure (e.g. Vekemans & Hardy, 2004). It has been suggested that indirect techniques tend to return much higher estimates of migration rates than direct techniques because the latter operate on spatially limited areas and ignore the contribution of long-distance dispersal (Koenig et al., 1996, but see Thompson & Goodman, 1997). Large differences of migration rates are therefore to be expected between direct and indirect techniques in organisms with long-distance dispersal (LDD) capacities, and, in particular, wind-dispersed species. Bryophytes, which primarily disperse by tiny spores of ca 10-20 µm, are typically seen as extremely efficient dispersers with strikingly large, disjunct distribution ranges (see Patiño & Vanderpoorten, 2018 for review).

In a recent study, Barbé, Fenton, and Bergeron (2016) found, based on comparisons between extant and propagule rain communities in residual forest patches, that several species from the propagule rain did not originate from the closest extant community and that there was little similarity between the extant and propagule rain communities, suggesting that regional dispersal events are important. These observations are in line with spore-trapping experiments, wherein spore densities quickly decrease with distance from the source, but wherein, with increasing

isolation, a higher proportion of spores originates from sources farther away than the nearest sources (Sundberg, 2005). In fact, Lönnell, Hylander, Jonsson, and Sundberg (2012) confirmed that the tail of the kernel, beyond 500m-1 km, is distance-independent. Such a 'fat-tailed' dispersal kernel could partly explain the wide distribution of many bryophyte species, the lack of an obvious distance effect on species richness on islands, the relatively low level of (allopatric) speciation in bryophytes as compared to seed plants, and the weak relationship between latitude and diversity (Sundberg, 2005; Sundberg, Hansson, & Rydin, 2006).

In such conditions of efficient short- and long-distance dispersal, an inverse isolation effect is predicted to develop (Sundberg, 2005; Barbé et al. 2016). An inverse isolation effect involves a higher genetic diversity of colonizing propagules with increasing isolation, thus counteracting differentiation. Consequently, no isolation-by-distance (IBD) is expected beyond a distance corresponding to short-distance dispersal events owing to the well-mixed and diverse propagule pool, except perhaps at very large scales, at which other factors, including geographic barriers and historical factors, might operate (Szövényi et al., 2012). Simulating the genetic consequences of efficient short- and long-distance dispersal on the decay of the kinship-distance curve, Hardy & Vekemans (1999) confirmed that, as the proportion of random long-distance dispersal m increases from 10^{-4} to 0.1, the IBD signal erodes progressively and becomes limited to the shortest distance ranges.

Such predictions have important ecological consequences because they suggest that spore dispersal cannot be described by a distance-dependent kernel, thereby challenging the application of integrative methods that have been increasingly developed to predict, from ecological niche models associated with explicit dispersal kernels employed to model species movements in a changing environment, future species distributions (Zurrell et al. 2016; Fordham et al. 2018).

In the present study, we performed a meta-analysis of the spatial genetic structure in bryophytes to test the hypothesis that efficient LDD erodes the impact of genetic drift, resulting in the absence of any IBD pattern beyond the nearest vicinity of the source.

Material and methods

We performed a literature review with Scopus, using 'isolation by distance' or 'spatial genetic structure' and 'bryophytes'. We obtained 16 studies informing on the spatial genetic structure for 28 species. From these studies, we managed to collect 38 datasets for 14 species, to which we added an expanded dataset for another 12 species from Désamoré et al. (2016). We employed Spagedi 1.5d (Hardy & Vekemans, 2002) to regress pairwise kinship coefficients Fij (Loiselle, Sork, Nason & Graham 1995) between individuals, or pairwise Fst when several individuals were sampled per locality, and the logarithm of pairwise geographic distances. The regression slopes were computed across the entire geographic range of the study on the one hand, and then for distance intervals between the successive distance limits: 0, 0.1, 1, 10, 100, 1000, and >1000 km (i.e. considering only pairs of individuals or populations separated by a distance <0.1 km, or between 0.1 and 1 km, or between 1 and 10 km, etc…). The significance of the slopes was tested by 1000 random permutations of individuals, or populations in the case of Fst, among localities across the entire geographic range (Mantel test). Within each distance interval, the significance of the slope was assessed by a Jack-knife test, wherein the slope was recalculated after successively pruning one locus from the data at a time to estimate the standard error of the slope. To assess the decay of the IBD signal at increasing distance intervals, we computed, for each

distance interval, the proportion of significant slopes, and used a t-test assuming unequal variances for comparing these proportions between adjacent distance classes.

Results and Discussion

Kinship coefficients significantly decreased with increasing logarithm of geographical distance between individuals in 35 out of the 42 datasets (Table S1). Non-significant tests were always associated with datasets lacking comparisons at the local (<1 km) scale, at which a significant structure was expected, except in the case of *Orthotrichum speciosum* (line 5 in Table S1), which Snäll et al. (2004) interpreted as a lack of statistical power of the Mantel test as compared to Generalized Additive Models. In fact, similar tendencies were observed with Fst, with 12 out of 20 significant tests (Table S2), but contrasting results were sometimes observed when the same data were analysed with Fst and Fij (contrast e.g. the results for dataset 31 in Table S1 and 17 in Table S2 and dataset 33 in Table S1 and 18 in Table S2). The two tests may hence have different statistical power, but it was not possible to determine under which circumstance one test performed better than the other. Nevertheless, it appears that, when isolation-by-distance tests are performed over a range including the local scale, a significant genetic structure emerges, in agreement with the observed higher spore densities within the close vicinity of the source (Sundberg 2005).

The decrease of genetic similarity with increasing distance was not uniform over the whole range of distances, as reflected by steep regression slopes at short distance ($\bar{b}_{<0.1}$=-0.07±0.06) shallower slopes at medium distances ($\bar{b}_{0.1-1}$=0.05±0.13, $\bar{b}_{1-10}$=-0.07±0.15, $\bar{b}_{10-100}$=-0.02±0.09, and a second shift of slope at large distance ($\bar{b}_{100-1000}$=-0.06±0.04, $\bar{b}_{>1000}$=-

0.07±0.06) (Table S1). A visual example of the differences of the slopes at different distance ranges is provided in the liverwort *Crossocalyx hellerianus*, with a striking decrease of kinship coefficients within the first 1km, then a flat relationship between Fij and distance until 1000km, and a second slope shift beyond 1000km (Fig. 1). The decay of the IBD signal is best illustrated by changes in the proportion of significant tests at increasing distance classes, with 91% of significant tests at a range of <0.1 km, followed by a subsequent significant decrease in the proportion of significant tests of 0, 33 and 31% at 0.1-1, 1-10 and 10-100km, respectively. At distances larger than 100km, the proportion of significant tests reached again >50% (Fig. 2). These results suggest that an inverse isolation effect, according to which the IBD signal is eroded with distance from the source due to random LDD, can be observed beyond the limit of short-distance dispersal reflecting the high spore densities within the first hundreds of meters from the source. Such a pattern is reminiscent of what is sometimes observed in angiosperms displaying steep IBD slopes at short distances, reflecting short-distance dispersal patterns of seeds, and shallow to non-significant slopes at larger distances, reflecting long-distance dispersal of pollen (Heuertz et al. 2003). The higher proportion of significant IBD patterns again observed at larger scales over 100 km likely marks the limits of regional dispersal, beyond which an increasingly smaller proportion of spores travel. Similar patterns were reported in ferns. In *Adiantum reniforme*, significant IBD slopes at a scale of 0.8-21km became non-significant when the two most distant populations were excluded (Kang et al. 2008). In *Asplenium*, Hunt et al. (2009) similarly interpreted the sharp slope shift observed beyond 50km in terms of random and rare LDD events at middle- and long-distance ranges. Such rare events across large distances of more than 100km are in particular thought to generate significant IBD patterns following the recolonization of northern areas that were glaciated 19,000 years BP from southern refugia

(Wang & Guan 2011, Bystriakova et al. 2014, Imai et al. 2016), although at such scales, the observed signal for IBD may be confounded with other factors, and in particular, geographic barriers.

While our results are thus consistent with the expectations of the inverse isolation hypothesis, according to which LDD erodes the signal of IBD at regional scales, they do not support the idea of a complete absence of genetic structure beyond the limits of SDD, as about 1/3 of the investigated datasets yield a significant IBD signal at regional scales (10-100 km from the source) and as an increasing proportion of tests reveals a significant spatial genetic structure beyond that scale. It therefore appears that, as opposed to Koenig et al. (1996), direct techniques based on spore-trapping experiments return higher estimates of migration capacities than indirect techniques based on spatial genetic structures. In fact, although Barbé et al. (2016) found species with a broad range of life-strategies in the spore cloud flora, the latter would, at first sight, include only the best dispersers, and it would be interesting to know which species are never represented in the spore cloud. Furthermore, spore-trapping experiments measure a rate of spore deposition, whereas analyses of spatial genetic structures reflect actual colonization rates. Even when fully developed gametophytes following spore germination were observed (Lönnel et al., 2012), the spore traps consist of patches of introduced bare ground that is compatible with the habitat preference of the target species, whereas spores landing in the wild face both environmental filtering and competition. Barbé et al. (2016) also grew airborne spores under laboratory conditions, so that the resulting flora may not necessarily match the set of species that would actually be able to establish on the ground. Munoz et al. (2013) similarly observed a mismatch between *I*, the effective number of immigrants competing with the offspring of a local community to replace a dead local individual in Hubbell's (2001) theory, and migration rates

186 estimates from experimental kernels. Munoz et al. (2013) suggested that such a mismatch
187 resulted from the integrative nature of *I* that, as do indirect estimates of migration derived from
188 spatial genetic structure analyses, represent an integrative index of migration limitation including
189 habitat filtering.
190 Finally, while the long-distance dispersal capacities of bryophyte spore are evident in light of
191 both phylogeographic (see Patiño & Vanderpoorten, 2018 for review) and experimental evidence
192 (Sundberg, 2005, 2013; Lönnel et al., 2012, 2014; Barbé et al., 2016), a significant spatial
193 genetic structure can emerge if actual colonization events take place during discrete windows of
194 opportunities. In mosses, spore release is controlled by the hygroscopic movements of the
195 peristome, which consists of a single our double layer of teeth at the mouth of the capsule.
196 Peristome movements are essential to regulate the dispersal of spores and play an active role in
197 closing and opening the mouth of the capsule depending on variation in air humidity and
198 vibrations caused by wind turbulence (Johansson, Lönnell, Sundberg, & Hylander., 2014;
199 Lönnell et al., 2015; Johansson, Lönnell, Rannik, Sundberg, & Hylander, 2016). Hygrochastic
200 peristomes open-up upon increasing relative humidity, when high chances of rain hamper the
201 chances of long-distance dispersal by wind, favoring short-distance dispersal as a safe-site
202 strategy in species from patchy and dynamic habitats (Medina & Estebanéz, 2014; Zanatta et al.,
203 2018), in line with the dispersal limitations evidenced by the analysis of genetic structures.
204 Xerochastic peristomes, in turn, open-up upon decreasing air humidity, which Johansson et al.
205 (2016) interpreted as an adaptive mechanism favoring the release of spores in the morning, when
206 the heating from the sun creates upward air movements. Moreover, wind turbulence is expected
207 to peak during episodes of storms, potentially transporting masses of spores from a specific
208 source area to a specific sink area during short period of time, resulting in a significant spatial

genetic structure. For example, phylogeographic evidence suggests that migrations between western Europe and the North East Atlantic islands are strongly asymmetric, from the islands to the continent, possibly taking advantage of discrete waves of storms crossing the Atlantic eastwards, whereas the trade winds are in the opposite direction (Patiño et al., 2015). Although we do not challenge the idea that bryophyte spore clouds efficiently travel across long, trans-oceanic distances (Sundberg, 2013), contributing to the striking range disjunctions typical of bryophyte species, the genetic data available to date are globally not compatible with the idea that intense long-distance migration events erase any signal of IBD in the data. We therefore conclude that geographic distance remains a significant proxy of spore colonization rates, with major consequences for our understanding of actual migration capacities in this group, and hence, our capacity to model range shifts in a changing world (Garcia, Klein, & Jordano, 2017). Further information on the contribution of short-and long-distance dispersal, the timing of dispersal events, and the importance of geographic barriers, would be necessary for better understanding spore dispersal patterns and assess the ability of spore-producing plants to efficiently track areas of suitable climate. In this context, we suggest that spatially explicit coalescent models (Dellicour, Kastally, Hardy & Patrick Mardulyn, 2014) represent a very promising tool to inform future predictions of range shifts from historical simulations.

Author contributions: AV, JP and OH designed the framework of the study. AD, BL, BP, HK, JK, and PG contributed data. AV and OH performed the statistical analyses. All the authors contributed to the writing of the manuscript.

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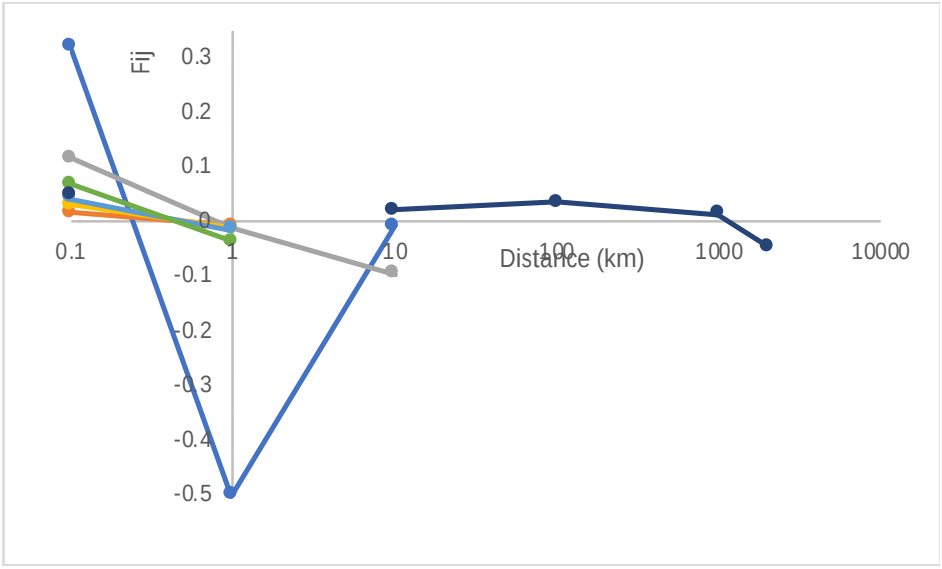
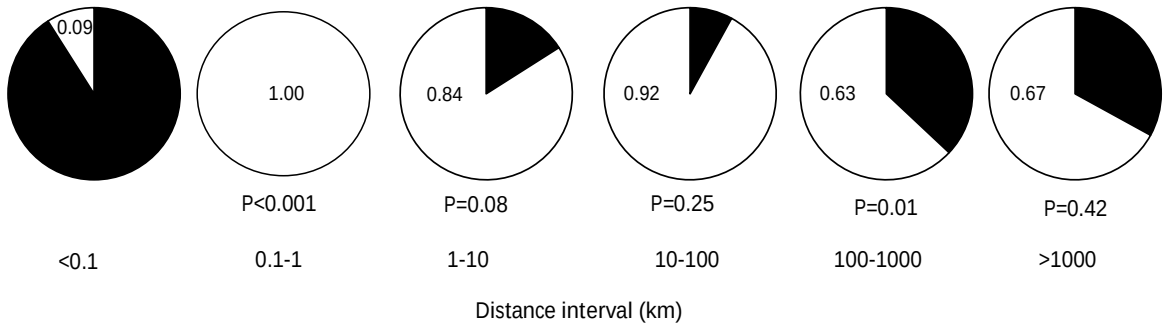


Figure 1. Average Fij values per geographic distance intervals in different populations of the liverwort *Crossocalyx hellerianus* at different spatial scales (recomputed from Hola et al. 2015).



424

425 Figure 2. Proportion of significant (in black) slopes of Fij and geographic distance for different
426 distance classes in a meta-analysis of spatial genetic structures in bryophytes (see Table S1). The
427 p-values correspond to t-tests between comparisons of adjacent distance classes.

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Table S1. Slope (± S.D.) and p-value of Mantel tests between Fij and log-distance in bryophytes. Shaded boxes represent the geographic range. 1-6 represent results from the literature and 7-42 were recomputed from data published in the references listed below. P-values are given for the entire range only and the significance of the slope per distance class is based on the jackknife across loci. Significant slopes are highlighted in bold. For unilocus data, the slope value is provided for information but these data are not used in the computation of significant tests.

		Slope b of F_{ij} on $\ln(d_{ij})$ within specific distance ranges					
N	Full range	0 - 0.1 km	0.1 – 1 km	1 – 10 km	10 – 100 km	100 – 1000 km	>1000 km
1.	**-0.019** P<0.001						
2	**-0.047** P<0.01						
3	**-0.058** P<0.001						
4	**-0.016** P<0.001						
5	NA P>0.05						
6	**-0.013** P=0.02						
7	**-0.065±0.0062,** P<0.001	**-0.065±0.006**					
8	**-0.136±0.014** P<0.001	**-0.088±0.006**					
9	**-0.239±0.015** P<0.001	-0.239±0.015					
10	**-0.056±0.01** P<0.001	**-0.102±0.012**					
11	**-.050±0.023** P=0.003	**-.050±0.023**					
12	**-0.013±0.006** P<0.001	**-0.013±0.006**					
13	**-0.012±0.002** P<0.001	**-0.015±0.004**	0.017±0.013				
14	**-0.015±0.0027** P<0.001	**-0.015±0.005**	-0.019±0.02				
15	**-0.013±0.003** P<0.001	**-0.021±0.004**	0.005±0.007				
16	**-0.065±0.0062,** P<0.001	**-0.046±0.006**	0.010±0.009				
17	**-0.043±0.006** P=0.032	**-0.118±0.04**	-0.046±0.046				
18	**-0.010±0.005** P=0.004		0.34±0.31	**0.10±0.026**	-0.018±0.016	**-0.044±0.019**	
19	0.019 P=0.83		0.032	0.043	0.058	-0.062	
20	-0.014±0.003			-0.062±0.033	-0.079±0.045		

	P=0.08						
21	**-0.010±0.004** P=0.012			-0.017±0.044	-0.004±0.007	-0.086±0.084	
22	-0.004±0.021 P=0.412			-0.09±0.08	0.007±0.015		
23	**-0.025±0.006** P=0.023			**-0.233±0.081**	-0.14±0.56		
24	**-0.053±0.008** p<0.001			-0.045±0.078	**-0.069±0.026**	**-0.098±0.026**	
25	**-0.128** p<0.001			-0.119	-0.080	-0.129	-0.074
26	**-0.035±0.0078** p<0.001			-0.035±0.31	-0.308±0.316	**-0.023±0.007**	-0.031±0.019
27	**-0.114±0.018** p<0.001			-0.009±0.032	-0.050±0.067	**-0.060±0.012**	**-0.105±0.01**
28	**-0.09±0.02** p<0.001			0.049±0.072	**0.063±0.025**	-0.072±0.047	**-0.084±0.032**
29	**-0.071±0.012** p<0.001			**-0.171±0.006**	**0.158±0.078**	-0.058±0.046	**-0.066±0.004**
30	0.002±0.002 P=0.75				0.002±0.002		
31	0.003±0.011 P=0.605				**0.023±0.003**		
32	-0.005±0.003 P=0.16				-0.005±0.003		
33	**-0.015±0.006,** P=0.006				0.034±0.018	0.001±0.073	-0.036±0.32
34	**-0.033** P=0.006				-0.056	-0.06	-0.015
35	**-0.089** P<0.001				-0.105	-0.053	-0.279
36	**-0.072±0.013** P <0.001				0.055±0.040	-0.0005±0.038	-0.021±0.026
37	**-0.050** p<0.001					-0.077	-0.038
38	**-0.094** p<0.001				-0.003	-0.043	-0.063
39	**-0.047±0.016** p<0.001				-0.045±0.123	**-0.068±0.027**	-0.007±0.020
40	**-0.033±0.007** p<0.001				0.043±0.06	-0.005±0.003	**-0.025±0.007**
41	**-0.139±0.045** p<0.001				**-0.083±0.027**	**-0.114±0.007**	-0.117±0.070
42	**-0.096±0.041** p<0.001				0.111±0.0097	**-0.114±0.044**	**-0.091±0.039**

1 *Rhynchostegium riparioides* (Hutsemékers et al. 2013). 2. *Calliergon megalophyllum* (Korpelainen et al. 2013). 3. *Fontinalis antipyretica* (Korpelainen et al. 2013). 4. *F. hypnoides* (Korpelainen et al. 2013). 5. *Orthotrichum speciosum* (Snäll et al. 2004). 6. *O. obtusifolium* (Snäll et al. 2004). 7. *Crossocalyx hellerianus*, pop. Y. (Hola et al. 2015). 8. Id., pop. G. 9. Id., pop. M. 10. Id., pop. N. 11. Id., pop. P. 12. *Barbilophozia*

attenuata (Korpelainen et al. 2011). 13. *Crossocalyx hellerianus*, pop. S (Hola et al. 2015). 14. Id., pop. V. 15. Id., Pop. K (Hola et al. 2015). 16. Id., pop. Z. 17. *Orthotrichum handiense* (Patino et al. 2013).). 18 *Sphagnum subnitens* (Mikulaskova et al. 2015). 19. *Bryum argenteum* (Pisa et al. 2013). 20. *Pleurozium schreberi* (Korpelainen et al. 2012). 21. *Rhynchostegium riparioides* (Hutsemékers et al. 2010). 22. *Plagiochila asplenioides* (Korpelainen et al. 2012). 23. *Rhytidiadelphus squarrosus* (Korpelainen et al. 2012). 24. *R. riparioides* (Hutsemékers et al. 2011). 25. *Metzgeria furcata* (Désamoré et al. 2016). 26. *Orthotrichum affine* (Désamoré et al. 2016). 27. *O. lyellii* (Désamoré et al. 2016). 28. *Timmia austriaca* (Désamoré et al. 2016). 29. *T. bavarica* (Désamoré et al. 2016). 30. *Sphagnum fallax* (Szövényi et al. 2012). 31. *S. fimbriatum* (Szövényi et al. 2012). 32. *S. palustre* (Szövényi et al. 2012). 33. *Crossocalyx hellerianus*, Poland+Finland (Hola et al. 2015). 34. *Pleurochaete squarrosa* ITS (Grundmann et al. 2007). 35. *Pleurochaete squarrosa* cpDNA (Grundmann et al. 2007). 36. *Amphidium mougeotii* (Désamoré et al. 2016). 37. *Calypogeia fissa* (Désamoré et al. 2016). 38. *Diplophyllum albicans* (Désamoré et al. 2016). 39. *Plagiothecium denticulatum* (Désamoré et al. 2016). 40. *P. undulatum* (Désamoré et al. 2016). 41. *Plagiomnium undulatum* (Désamoré et al. 2016). 42. *Scorpiurium circinatum* (Désamoré et al. 2016).

Table S2. Slope (± S.D.) and p-value of Mantel tests between Fst and log-distance in bryophytes. Shaded boxes represent the geographic range. 1-9 represent results from the literature and 10-20 were recomputed from data published in the references listed below

	Full range	<10 km	10-100km	100-1000km	>1000km
1	NA P=0.30				
2	NA P=0.06				
3	**1.08 P<0.01**				
4	0.07 P=0.13				
5	**1.39** P<0.01				
6	**2.51** P<0.01				
7	**0.86** P<0.01				
8	**0.16 P=0.02**				
9	**NA P<0.001**				
10	0.012±0.015 P=0.30	**0.09±0.04**	-0.234±0.169		
11	-0.031±0.028 P=0.41	0.070±0.111	-0.016±0.035		
12	**0.048±0.022** P<0.001	**0.208±0.05**	0.57±0.31		
13	**0.026±0.017 P=0.028**	-0.001±0.007	-0.003±0.013	0.113±0.17	
14	**0.052±0.014 P<0.001**	-0.264±0.167	0.007±0.026	**0.103±0.039**	
15	-0.003±0.004 P=0.37		0.002±0.002		
16	-0.020±0.022 P=0.11		-0.020±0.022		
17	**0.022±0.006 P=0.006**		**0.022±0.006**		
18	0.003±0.007 P=0.35		**0.188±0.02**	**-0.017±0.08**	-0.595±0.316

19	**0.051 P=0.002**		0.064	0.029	0.108
20	**0.081 P=0.002**		0.096	-0.032	0.17

1 *Hylocomium splendens* (Cronberg 2002). 2. *Leptodon smithii* (Spagnuolo et al. 2007). 3. *Sphagnum angustifolium* (Kyrkjeeide et al. 2016). 4 *S. austinii* (Kyrkjeeide et al. 2016). 5 S. *fuscum* (Kyrkjeeide et al. 2016). 6 *S. quinquefarium* (Kyrkjeeide et al. 2016). 7 *S. rubiginosum* (Kyrkjeeide et al. 2016). 8 *S. wulfianum* (Kyrkjeeide et al. 2016). 9. *S. miyabeanum* (Shaw et al. 2014). 10 *Pleurozium schreberi* (Korpelainen et al. 2012); 11 *Plagiochila asplenioides* (Korpelainen et al. 2012). 12 *Rhytidiadelphus squarrosus* (Korpelainen et al. 2012). 13 *Rhynchostegium riparioides* (Hutsemékers et al. 2010). 14 *R. riparioides* (Hutsemékers et al. 2011). 15 *Sphagnum fallax* (Szövényi et al. 2012). 16 *S. fimbriatum* (Szövényi et al. 2012). 17 *S. palustre* (Szövényi et al. 2012). 18 *Crossocalyx hellerianus* Poland+Finland (Hola et al. 2015). 19 *Pleurochaete squarrosa*, ITS (Grundmann et al. 2007). 20 *P. squarrosa*, cpDNA (Grundmann et al. 2007).